

THE VAPOR TENSION RELATIONS OF FROGS

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INTRODUCTION

An account of the water relations of frogs would be incomplete without a description of the exchanges of vapor between the animals and environing atmospheres. Some of the same properties of osmotic pressure and permeability that control water exchanges when frogs are surrounded by liquid might be expected to exhibit themselves in the presence of air. But whereas liquid water may serve as a medium for the exchange of other substances, water vapor is lost from the body without being accompanied by any dissolved material.

The two chief objects of the observations were: first, to find whether the rate of evaporation from the frog's body is proportional to the relative humidity of the atmosphere, or at least fixes a vapor tension curve for the organism; and second, to find whether a frog can come into equilibrium with a definite vapor tension. In theory every object has a measurable vapor tension; in practice the relation to water vapor is greatly complicated by the thermal properties of the body. It therefore becomes necessary to interpret data on rates of evaporation in terms of heat production, body temperature, and thermal conductivity.

Of practical consequence is the finding that under no circumstances can a frog absorb water from the atmosphere. Taken in connection with the fact that the skin offers no unusual obstruction to the loss of water into the atmosphere, it is evident that with respect to water balance a frog is unsuited to non-aquatic existence.

METHODS

In the course of the experiments six different procedures were used to establish the relationship between the frog and the atmosphere. Each method was instructive upon certain points and each was useful to evaluate some factors of water exchange. All the methods depended upon weighing the frog at frequent intervals; in these intervals only water was lost in appreciable amounts. The loss of carbon by a frog of 30 grams weight amounts to about 1.3 milligrams per hour, calculating from the mean rate of carbon dioxide production,

measured by Smith (1925) on *Rana pipiens*. The same species was used in all the present measurements of evaporation.

The six methods of weighing evaporation losses that were used will be designated by letters. The last one is to be recommended for most general use in the study of atmospheric relations of organisms.

A. Frogs were exposed to the air of the room in a wire basket resting on a table. The temperature, relative humidity, and dew-point of the air were read at intervals. With inappreciable air motion and small changes of humidity during any one test, the weight changes could be related to the average humidity for the period.

B. A single frog was enclosed in a 400 cc. glass chamber through which conditioned air was recirculated. The chamber was suspended from a triple-beam balance, and connected by flexible rubber tubes with wash-bottles containing sulphuric acid mixtures. The air was pumped by raising and lowering a mercury bulb by means of a "wind-shield wiper"; the wash-bottles, in the bottoms of which were layers of mercury, serving as the valves of the pump. The apparatus was run in a room of constant air temperature, but this did not prevent water from condensing in the chamber when high humidities were used.

C. A single frog was placed in a screen cage in a 4-liter jar equipped with a fan. The fan was spun very rapidly by a belt and motor outside the jar, the fan shaft piercing a brass top fitted by a groove to the jar. The fan was stopped and the jar was opened each time the frog was to be weighed. In the bottom of the jar was a sulphuric acid mixture which controlled the relative humidity of the air. The fan and the air movement produced considerable heat so that temperature gradients always existed. The steady state was temporarily destroyed at each removal of the frog for weighing. The apparatus was operated in the constant temperature room.

D. The fan chamber was used, but the cage containing the frog was suspended from the balance arm by three wires passing through three holes in the chamber lid. The holes were closed by felt washers except when weighings were being made, at which time the fan was also stopped. The chamber was immersed in a regulated water-bath up to the rim, but most of the heat gradients persisted.

E. The frog rested on a screen platform in an ordinary desiccator above a sulphuric acid mixture. The desiccator was immersed in the water-bath up to the rim and was opened to remove the frog at each weighing. In weighing, the frog was exposed to another atmosphere and to handling, and the results were therefore unreliable at slow rates of drying. The air was quiet except as it was moved by the frog's breathing, but the frog remained at a constant distance (5 cm.) from the equilibrating solution.

F. A frog was suspended in a jar by a single wire from a balance arm. The jar and top were completely immersed in a water bath. The wire passed through a vertical tube in entering the jar, and the tube was ordinarily closed by a washer on the wire; when a weighing was taken the wire was raised slightly. The weights were reproducible enough so that an analytical balance was used. The cage proved to be a complicating factor because water coated its wires through capillary attraction away from the frog's skin. The most constant results were obtained by pithing the frog and suspending it by fine wires in a horizontal position. This method was accurately checked by exposing solutions of diverse vapor tensions in a glass dish in place of the frog.

High humidities were obtained by exposing the air to water or salt solutions of known concentrations. Lower humidities were controlled by keeping the air in contact with mixtures of sulphuric acid and water; their concentrations were estimated from their specific gravities measured with a Westphal balance. The vapor

tensions of all these solutions were obtained from chemical handbooks.

Recovery from desiccation was studied in about half of the experiments. The frogs were placed in tap water and weighed at frequent intervals in the manner usual for wet frogs (Adolph, 1931).

RATES OF EVAPORATION

Frogs were gently blotted with a towel before each experiment so that no water would drip from their surfaces. Urine was pressed out of the bladder in the course of handling them, and it is well known that urine formation ceases when water is no longer being taken into the body (Adolph, 1927). Under these circumstances regular changes

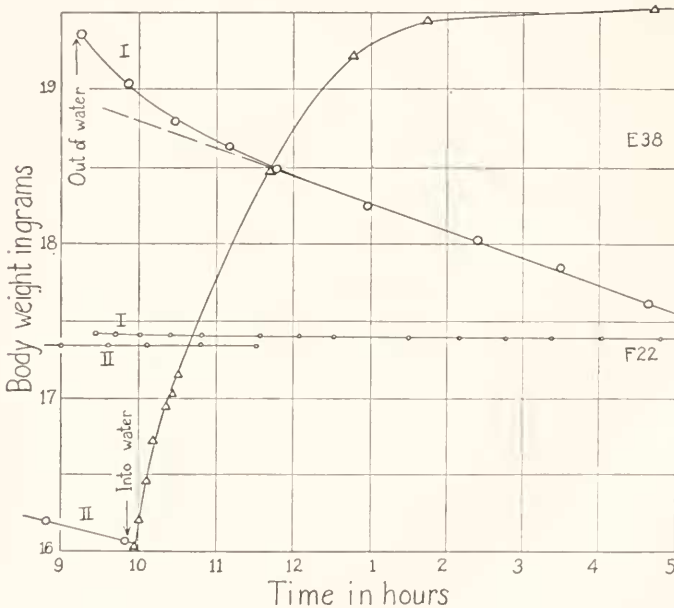


FIG. 1. Changes of body weight during evaporation (by method *E*) and recovery in tap water. The evaporation occurred in an atmosphere saturated with moisture at 20° C. during 25 hours, with slight decrease in rate throughout. For comparison of methods, the rate of evaporation by method *F*, during 26 hours exposure to a saturated atmosphere at 20° C., is also shown. In each case *I* and *II* represent successive days, each experiment being continued through the intervening night.

of body weight were observed. Temperature adjustments all occurred within the first half-hour; then weight was lost rapidly for one or two hours, after which the rate of loss was quite constant from hour to hour. This series of events is shown for one experiment in Fig. 1. Within the next 24 hours the rate of weight loss in any humidity usually decreased very slowly. This change of evaporation rate was

as great as 50 per cent when the atmosphere was saturated, but was less than 20 per cent when the humidity was nearly zero.

The responses of a single individual upon successive exposure to diverse humidities is shown in Fig. 2.

The various experiments were compared by plotting the rates of evaporation against the relative humidities that prevailed. It may be stated that no object is known for whose vapor equilibrium the absolute humidity has significance apart from the relative humidity. This principle follows from the kinetic behavior of gases at uniform temperature. In the experiments it was assumed that the relative humidity was that which would have prevailed if the atmosphere were completely in equilibrium with the equilibrating liquid; this liquid always exposed more surface than the frog. In many experiments a hair-hygrometer was placed in the chamber with the frog and this assumption was found to be nearly true.

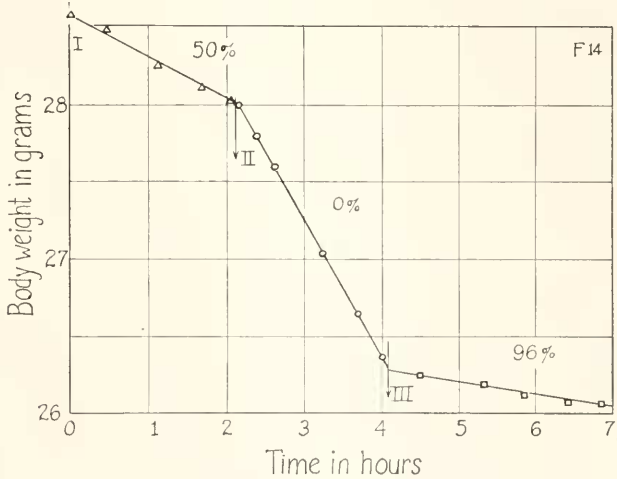


FIG. 2. Changes of body weight during successive exposures (by method *F*) to three relative humidities.

The rates of evaporation may be estimated in a number of ways; by finding the percentage of the original body weight lost in 24 hours, or the average number of grams of water lost per hour in the first six hours, or the grams per square centimeter of body surface lost during the steady state of the third to seventh hours of an experiment. Actually the experimental results were analysed in these several ways, and the last one was adopted, both as giving the most consistent and reproducible data and as being the most rational.

All the results by the six methods are shown as averages in Fig. 3.

Since the rates of evaporation by three different methods fall on curved lines, it is probable that the rates are not exactly proportional to relative humidities. This may be due to some feature of the experiment such as the gradient of vapor near the frog's skin and is not necessarily to be ascribed to the supply of moisture on the surface of the body. One important factor is that, as Hall and Root (1930) observed, the body temperature is much lower than the air temperature as the humidity declines.

A serious attempt was made to relate the rates of evaporation in high vapor tensions to the rates of water exchange by the frog im-

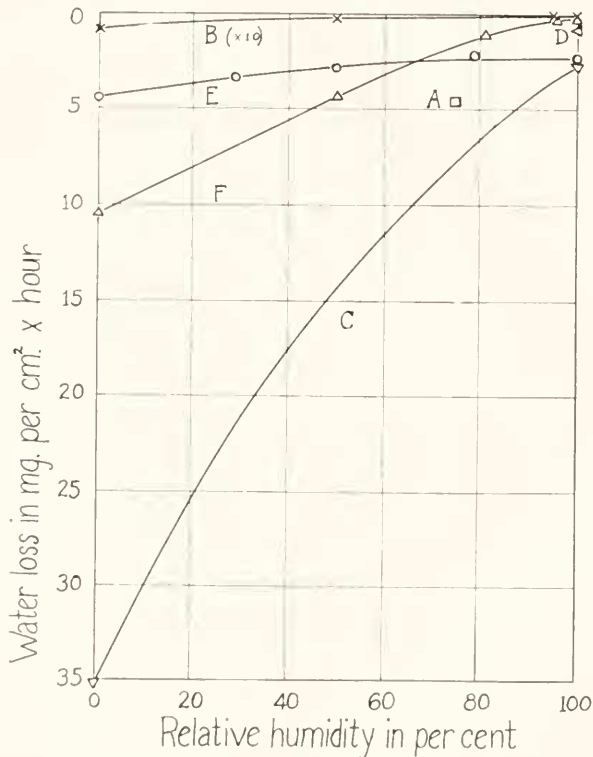


FIG. 3. Mean rates of evaporation at various relative humidities as obtained by the six methods.

mersed in salt solutions of the corresponding tensions. It is well known (Durig, 1901; Adolph, 1925) that in a certain range of sodium chloride solutions that are hypotonic when compared with the body fluids of the frog, water is gained by the body faster than it is gained in tap water. Was it possible that the vapor tension of the frog was higher at 99.8 per cent relative humidity than at 100 per cent? When

compared (by method *C*), no significant difference in rate of evaporation was found at these two humidities. But this merely meant that the precision of the method was too low. In fact none of the methods was nearly good enough to decide this point, because the evaporation was slow even with high velocities of air motion, and because the production of heat by the frog as well as by the air motion could not be sufficiently corrected for.

VAPOR TENSION EQUILIBRIUM

Is it possible to establish conditions in which a frog will neither gain nor lose water? The only procedure sufficiently accurate to answer this question was method *F*. Some 30 experiments were run with saturated atmospheres; the air temperature being constant to $\pm 0.01^\circ \text{C}$., and fluctuations of weight due to all causes being reduced to ± 0.5 milligram per hour. The average result was a loss of 4.3 milligrams per hour by the frog, or perhaps 3.0 milligrams if the loss of carbon is allowed for. In 5 of the experiments slight gains of weight were shown and in 6 more experiments no change of weight occurred. But in every one of these 11 tests water was later found on the wire cage, and in all experiments where the wire cage was omitted and the pithed frog merely hung in the chamber some weight was lost. A few experiments where the humidity was reduced to 99.7 and 99.3 per cent showed similar losses of weight from the frog.

It is believed that no means could be devised of bringing a living frog into vapor tension equilibrium. The reason for this is, of course, that the organism is producing heat, and that at the frog's surface exists therefore a slight vapor deficit. A frog weighing 30 grams produces 12.5 calories per hour (Smith, 1925), and has a body surface of about 75 sq. cm. (Adolph, 1931); hence in a steady state it is losing 0.17 cal. per sq. cm. per hour. The evaporation from the frog of 4.3 milligrams of water per hour is equivalent to an expenditure of latent heat of 0.034 cal. per sq. cm. per hour. In other words, even this rate of evaporation dissipates only one-fifth of the heat that is being basally produced. Moreover, it eliminates between two and three times the amount of water that is being basally produced in the frog's body by oxidation, which is 1.6 milligrams per hour. The loss of 20 per cent of the frog's metabolic heat by evaporation in this atmosphere happens to be similar to the loss of 24 per cent of a man's metabolic heat by evaporation under basal conditions. It is obvious that no vapor equilibrium can be approached more closely than this by the metabolizing organism.

EFFECTS OF PITHING AND OF REMOVAL OF SKIN

The best determinations of evaporation rate, as already stated, could be made when the frog was totally quiescent and when the frog could be suspended by fine wires instead of being put into a cage. A few experiments were therefore made to compare the pithed frog with the normal frog. This was best done at high rates of evaporation, because of the smaller importance of absolute errors under such conditions. One experiment is shown in Fig. 4, and it is evident, as was true in other similar experiments, that no consistent difference existed in rates of evaporation between the pithed and the normal frog. A similar conclusion was reported by Hug (1927).

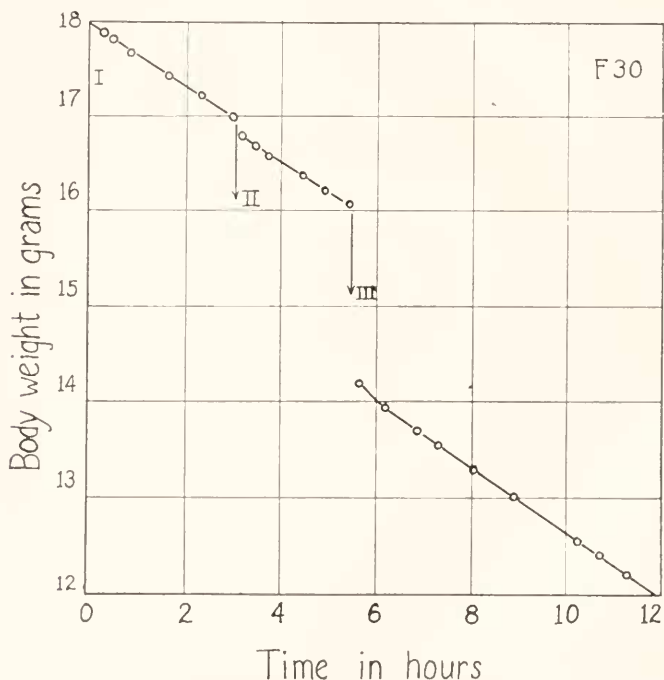


FIG. 4. Changes of body weight during successive exposures of the same frog under three conditions to a relative humidity of 50 per cent. *I*, normal; *II*, pithed; *III*, skinless. Method *F*.

After each experiment it was ascertained that the circulation of the blood persisted in the pithed individual. Two tests in which the circulation was completely stopped showed no detectable difference from the normal frog, and it is likely that the circulation is not a limiting factor in the rate of evaporation. It was concluded by Hug (1927) that dead frogs evaporated at the same rates as living ones.

During and after the evaporation tests it was noted that the appearance and feel of dryness in the skin was highly variable. But it proved impossible to correlate this condition with the rate or the amount of desiccation suffered.

In a short series of experiments the entire skins were removed from pithed frogs. It seemed possible that the external surface of the skin, being in equilibrium with fresh water, would naturally have the vapor tension of pure water, while the deeper tissues would have vapor tensions similar to that of a Ringer's solution, which corresponds to 99.7 per cent relative humidity. It was found that in low humidities the rate of evaporation of a skinless frog was little different from the rate of a normal frog, as Fig. 4 shows. This is in marked contrast to the protection against evaporation furnished by the skins of reptiles (Gray, 1928).

In saturated atmospheres also no difference of rates could be measured. Whereas normal frogs lost 4.3 milligrams per hour, six skinless pithed frogs lost on the average 3.6 milligrams per hour, which is a much better agreement than could be expected. Obviously the heat production of the frog is sufficient to prevent water from condensing on the superficial tissues even though its vapor tension be slightly lower than the tension of pure water.

In a number of experiments frogs were first desiccated by 15 to 35 per cent of their body weights and then placed in saturated atmospheres. In no case was there a significant gain of weight; on the average the rate of loss was the same as for a normal frog. Even when the desiccated frogs were pithed and skinned no gains of weight were found. Evidently the vapor tension of the body cannot by this means be lowered sufficiently to overcome the vaporization due to dissipation of metabolic heat.

RATE OF REGAIN OF WATER AFTER DRYING

But when put into water, a desiccated frog regains fluid at a rapid rate. The course of this regain is shown for one experiment in Fig. 1. The rate is fairly uniform for the first hour or two hours, though some gradual diminution in rate occurs. After the original weight of the frog has been attained, the gain ceases quite sharply.

The average initial rate of gain (38 experiments) was 0.8 gram per hour or 11 milligrams per square centimeter of body surface per hour. This is more rapid than the fastest desiccation in still air can be accomplished. The rate of regain is not correlated with the amount of desiccation, provided at least 5 per cent of the body weight had been lost, nor with the velocity of the desiccation.



Partial contact of the body with moisture is sufficient to supply water for regain (Stirling, 1877; Durig, 1901). If the dried-out frog is merely placed on a damp towel, water will be imbibed through the skin at the average rate. So far as is known to investigators generally, frogs never ingest water through the mouth when immersed in it.

It is of interest that the rate of respiratory metabolism increases with moderate desiccation of the frog and decreases markedly with extreme desiccation (Caldwell, 1925).

HEAT EXCHANGES

It has been demonstrated that the exchanges of water between frog and atmosphere do not correspond to an ordinary vapor equilibrium. The explanation is found in the continual production of heat in the body. In an atmosphere saturated with moisture at

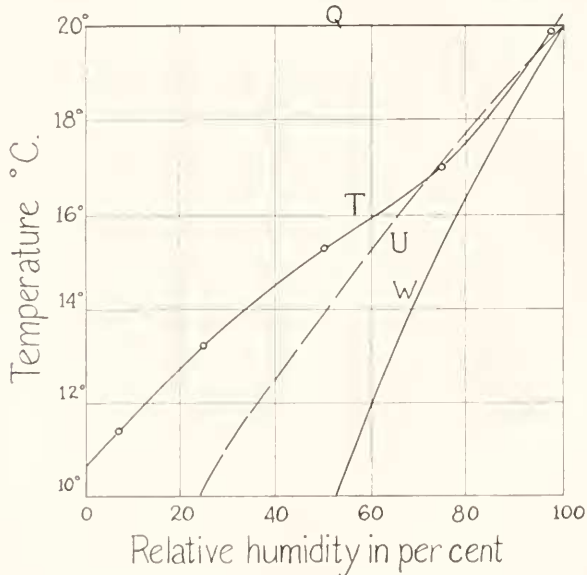


FIG. 5. Humidity and temperature relations at 20° C. *Q*, dry-bulb temperature of the air; *T*, rectal temperature of *Rana pipiens*, data taken from Hall and Root (1930); *U*, wet-bulb temperature of the air; *W*, dew-point temperature of the air.

exactly body temperature this heat cannot be lost by radiation, nor by conduction, nor by convection. Evaporation is also impossible. Hence heat accumulates in the body until the surface temperature rises above that of the surroundings. With each fraction of a degree rise in temperature of the body, more conduction, convection and radiation become possible. The higher temperature now makes possible also evaporation into the warmed layer of air adjacent to the skin.

The body temperatures of frogs in various relative humidities at 20° C. are supplied by the data of Hall and Root (1930); they are replotted in Fig. 5. The vertical distance between the lines *T* and *W* in this figure is the difference of temperature that exists in a steady state between a frog's body and the dew-point of the air surrounding it. This is least at 100 per cent humidity (0.25°), as might be expected.

Comparison with the wet-bulb temperature as obtained with a standard psychrometer (*U*), shows that a frog resembles a wet-bulb

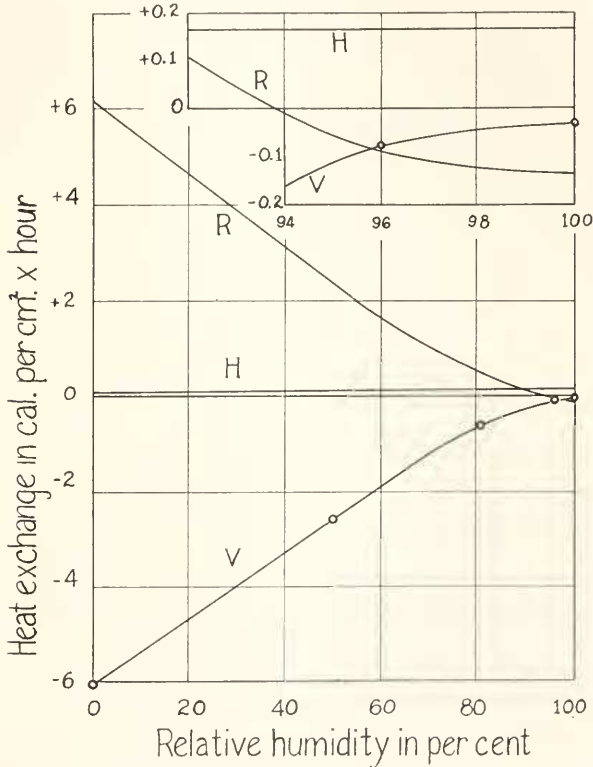


FIG. 6. Partition of virtual heat exchanges by frogs at 20° C. *R*, gain of heat by conduction, convection, and radiation from the surroundings; *H*, gain of heat by oxidative production in the frogs; *V*, loss of heat by evaporation of water from the frog's surface. The inset at the top is a ten-fold enlargement of the right-hand edge of the graph.

thermometer very closely in high humidities. In low humidities the effect of convection in slinging the psychrometer is more pronounced. Hall and Root (1930) had only slight air movement when they measured the rectal temperatures of the frogs.

Evaporation as a complication of measurements of heat production has been discussed, at least for isolated tissues (Fischer, 1927; Hill, 1930). Heat production as a complication of measurements of evaporation deserves equal recognition.

From the rates of evaporation into air of diverse humidities it is now possible to estimate the proportions and total amounts of heat dissipated by vaporization on the one hand, and conduction, convection and radiation on the other hand. It is assumed for this purpose that all the water evaporated from the body gained its latent heat from the frog; this is very nearly true because the specific heat of the body is much higher than that of the air surrounding it. The view is equally sound that the frog really receives no heat from the surroundings while in the steady state, but merely acts as a converter of kinetic heat into latent heat within the atmosphere.

The calculations of heat production are facilitated by the data of Hall and Root (1930) on the body temperatures of frogs in various humidities (Fig. 5), and by the numerous data, as those of Vernon (1897) and Krogh (1914), on the relative rates of respiratory metabolism at various temperatures.

The partition of heat losses from the frog is indicated in Fig. 6, the rates of loss by evaporation being calculated from the measurements by method *F*. It will be seen that under nearly all atmospheric conditions evaporation alone removes heat much faster than combustion generates it. Ordinarily, therefore, the frog is virtually taking up heat from the surroundings by conduction, convection and radiation. It has been ascertained in the present experiments that in 100 per cent humidity, however, the evaporation accounts on the average for only one-fifth of the heat loss. Since the cooling is all produced by evaporation in proportion to the difference of vapor tensions between the frog's surface and the air, it is easily understood why there is no condensation of water on the surface of the frog even though it is much cooler than the atmosphere. The temperature of the frog never decreases to the dew-point of the atmosphere that surrounds it.

It is also possible to calculate roughly a coefficient of heat flow for the combined virtual losses by conduction, convection and radiation, excluding evaporation, from the data of Fig. 6. The heat dissipation (H') is proportional to the body surface (S) to the time (t), and to the temperature difference (θ). Or

$$H' = kSt\theta.$$

The best value of k , for the range of low humidities where k is actually

constant, calculated from the slopes of line *R* in Fig. 6 and line *T* in Fig. 5, is 1.0 cal. per square centimeter per hour per degree centigrade. It is more than possible that the curves present in the line for body temperatures (Fig. 5) and in the line for evaporation rates (Fig. 6) are significant, in which case *k* is modified at diverse high relative humidities, and the thermal properties of the frog's body differ at various humidities or body temperatures. Such differences might be due to vasomotor shifts or other physiological responses.

The amount of this heat flow that is due to the single factor of radiation can be calculated. It is assumed that the frog has maximal radiation (as for an ideal black body) such as is believed to hold true for human skin (Cobet, 1924), and that 70 per cent of its surface is exposed to radiation. It is then found that this form of heat transfer might account for half of the combined heat flow (*R*) at low humidities and for all of it at humidities above 70 per cent. Further, it can be calculated from the constant for heat conduction through air that a still atmosphere would be unable to conduct much of the other half of the heat from the water of the bath to the suspended frog. Hence convection currents set up by the frog's breathing and by temperature differences near the body must be important in bringing heat to the animal.

COMMENT

The failure of frogs to absorb water from moist atmospheres means that these animals cannot survive long away from liquids. While the habits of frogs are such as usually to keep them in or near water, toads are ordinarily regarded as terrestrial. Toads, when subjected to similar vapor tensions, likewise showed no ability to absorb vapor from a saturated atmosphere. Their survival away from water evidently depends upon their taking up water while in contact with wet objects; it has been seen that mere moisture held in towels can supply this. Soil is a sufficient natural source of supply. So far as is now known, a toad has no properties fitting it for water conservation or accretion that are not possessed by most aquatic animals.

The amounts of desiccation endured by frogs have always been matters for remark ever since the first observations were made by Edwards (1824), Chossat (1843) and Kunde (1857). Various investigators have attempted to find how much loss of water is consistent with subsequent recovery; loss of roughly 40 per cent of the body weight, which is 50 per cent of absolute water content, allows of survival (Snyder, 1908; Hall, 1922; Smith and Jackson, 1931).

Studies have been made of the relative losses by the various organs and tissues of the frog's body during desiccation (Durig, 1901;

Ueki, 1924; Iizuka, 1926; Smith and Jackson, 1931). At present little relation can be deciphered between the partition of water losses and the water economy of the body as a whole. It is possible that the marked loss of water by the skin helps to diminish the rate of subsequent evaporation to the small extent found above.

SUMMARY

1. Frogs lose water by evaporation at rates that are nearly inversely proportional to the relative humidities of atmospheres.

2. Functioning of the central nervous system, of the blood's circulation, and of the skin made no significant differences in rates of evaporation.

3. In saturated atmospheres evaporation still goes on, which is explained by the fact that the production of heat keeps the body slightly warmer than the atmosphere.

4. In unsaturated atmospheres heat may be regarded as being lost by evaporation until the lowered temperature of the body comes into a steady state with the gain of heat by conduction, convection, and radiation from the surroundings.

5. No equilibrium of zero evaporation can be established for the living frog, and so the vapor tension of the frog's surface cannot be measured.

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